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Review paper

Structural attributes of stand overstory and light under the canopy

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Abstract - This paper reviews the literature relating to the relationship between light availability in the understory and the main qualitative and quantitative attributes of stand overstory usually considered in forest management and planning (species composition, density, tree sizes, etc.) as well as their changes as consequences of harvesting. The paper is divided in two sections: the first one reviews studies which investigated the influence of species composition on understory light conditions; the second part examines research on the relationships among stand parameters determined from mensurational field data and the radiation on understory layer. The objective was to highlight which are the most significant stand traits and management features to build more practical models for predicting light regimes in any forest stand and, in more general terms, to support forest managers in planning and designing silvicultural treatments that retain structure in different way in order to meet different objectives.

Keywords - Understory light, structural attributes, overstory stand, forest management

Introduction

The recognition of forest as complex system among scientists and communities (Levin 1998, Kuuluvainen 2009, Ciancio and Nocentini 2011, Puettmann et al. 2013) has increasingly raised the necessity to develop new strategies for managing woodlands and make them more suited to face the challenges of global change (Franklin et al. 2002, Larsen and Nielsen 2007, Millar et al. 2007, Puettmann 2011, O'Hara and Ramage 2013, Wagner et al. 2014). Different approaches, new tools and decision criteria on analyzing forest stands and designing silvicultural systems are being developed and improved (O'Hara 1998, Koch and Skovsgaard 1999, Gamborg and Larsen 2004, Pommerening and Murphy 2004, Meitner et al. 2005, Puettmann et al. 2009, Geldenhuys 2010, Messier & Puettmann 2011, Bradford and Kastendick 2010). Most of proposals aim to get multi-aged, mixed forests with heterogeneous structure consisting of a fine-scale mosaic of cohorts of trees, with different species, size, age and development stage and temporal continuity of natural regeneration of trees. Single and group selection silvicultural systems with very variable retention of live and dead trees, emulating natural disturbance regimes, were proposed in order to modify overstory cover and create spatially differentiated microclimate conditions, particularly in terms of understory light availability. Light directly or indirectly affects other environmental parameters such as temperature, humidity, wind speed, soil condition, and can be even an effective indicator of the differences in stand structure across forests (Larcher 2003).

Foresters are aware that understory light availability plays a crucial role in driving forest dynamics, since it influences several aspects of plant regeneration and growth processes, such as seed germination, plant recruitment, early establishment of seedlings, young tree survival (Beaudet et al. 2011, Bartemucci et al. 2006). The benefits of managing light levels in the understory also include the control of shrub/herb layers growth either to suppress them as competitors or to promote their richness as source of biodiversity (Lieffers et al. 1999, McKanzie et al. 2000, Whigham et al. 2004, Royo and Carson 2006, Hart and Chen 2006, Gilliam et al. 2007, Moelder et al. 2008, Tinya et al. 2009).

The importance of light in forest ecology justifies the attention that researchers have devoted to it. A considerable work in reviewing knowledge on description and prediction of understory light was done by Lieffers et al. (1999). The paper synthesized much literature relating to light dynamics in northern and boreal forests, considering the factors affecting light transmission through the canopy, instruments and techniques for measurement and models for prediction of light in stands. Objective estimation of light transmission in different stand structures would be very useful to support the ap-

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plication of silvicultural treatments that aims to modify light conditions within stands by thinning (Chianucci and Cutini 2012, Drever and Lertzman 2001). However, the high cost of instrumentation and more time-consuming procedures required to estimate factors to use as model inputs (e.g., foliage inclination distribution, foliage clumping, canopy structure and stem mapping) often favoured the use of more readily available mensurational variables as independent variables.

Over the last two decades, several articles have been dedicated to the relationship between light availability in the understory and the main qualitative and quantitative attributes of stand overstory usually considered in forest management and planning (e.g., species composition, density, tree sizes, etc.) as well as their changes as consequences of harvesting (e.g., Canham et al. 1990, Chianucci and Cutini 2013, Lieffers et al. 1999, Thomas et al. 1999). We reviewed such literature to individuate the most significant stand traits and management features able to predict light regimes in any forest stand; such information would support forest managers in planning and designing silvicultural treatments that retain structure in different way in order to meet different objectives.

The paper is divided in two sections: the first one reviews studies which investigated the influence of species composition on understory light conditions; the second part examines the relationships among stand parameters determined from mensurational field data and the radiation on understory layer.

Forest composition and understory light

Silvicultural practices modify tree species composition, simultaneously modulating overstory canopy cover and therefore the availability of light under the canopy (Barbier et al. 2008, Chianucci and Cutini 2013).

Light transmittance also varies considerably among tree species, partly because their light demanding strategies (Montgomery and Chadzon 2001), so that the relative proportion of some categories of species (deciduous or coniferous, shade tolerant or intolerant) in mixed stands may explain, at least in part, the spatial and temporal variability of understory light (Hart and Chen 2006, Barbier et al. 2008). Light demanding species (both deciduous and coniferous) transmit more light than shade tolerant species; in terms of canopy attributes, these species generally exhibits lower canopy density, higher between-crowns clumping (canopy nonrandomness) and higher crown porosity (the fraction of gap within crown envelopes; Kucharik et al. 1999). Conversely, shade tolerant species can reach higher canopy density, less between-crowns clumping and lower crown porosity (Chianucci and Cutini 2013, Macfarlane et al. 2007), with resulting lower light transmittance (Canham et al. 1994, Messier et al. 1998, Messier et al. 1999, Beaudet et al. 2002, Coates et al. 2003, Le Francois et al. 2008).

Forest canopy structure and light transmittance in mixed-species stands are the results of complex interactions which may lead to denser canopy space filling and more complete light interception (Pretzsch and Schütze 2005). However, not all studies came to the same results: Drever and Lertzman (2003), in coastal Douglas-fir stands that varied in abundance and distribution of retained trees after partial cutting of different intensity, found that species composition was only weakly related to the amount of light in the understory. In that case the higher canopy openness than in intact forests dominated by different species (Canham et al. 1994, Hunter et al. 1999) highlighted that in managed forests other structural features affect light availability in the understory.

Among the canopy properties, spatial arrangement of branches and leaves, leaf angle distribution and leaf orientation, leaf size and other optical properties of leaves, play an important role in affecting overstory transmittance (Valladares and Pearcy 1999, Falster and Westoby 2003, Hardy et al. 2004, Gendron et al 2006, Barbier et al. 2008) as indicated by the Beer-Lambert's law (Equation 1, based on Nilson 1971):

$$P(\theta) = \exp\left(\frac{-G(\theta) \times L_t \times \Omega(\theta)}{\cos\theta}\right) \quad (1)$$

Where $P(\theta)$ is the radiation transmitted through the canopy, $G(\theta)$ is the foliage projection function, which is dependent on leaf angle distribution, L_t is the plant area index, including foliar and woody vegetation, (θ) is the foliage clumping index an $1/\cos(\theta)$ is the path length at zenith angle θ. The inversion of Beer-Lambert law is often used to extract many of these attributes (Chianucci et al. 2014b, Nilson 1999, Monsi and Saeki 2005, Pisek et al. 2013) from optical measurements of radiation.

Aussenac (2000) showed that the inclination angle of leaves with respect to canopy thickness, for *Fagus sylvatica* L. and *Quercus petraea* Liebl., follows Beer's law, and also that beech adapts better to excess and very low radiation than oak. This type of tropism can also be seen in conifers. Species exhibiting more horizontal leaf angle distribution intercept more light than species having more vertical distribution. Some studies (Oker-Blom and Kellomaki 1982, Pisek et al. 2013) have shown that broadleaf species at northern latitude exhibit a planophile leaf angle distribution (i.e., leaves have predominantly horizontal leaf angle distribution). Hikosaka and Hirose (1997) observed a greater capacity of species with planophile foliage orientation to shade out the species with vertical foliage orientation while simultaneously having a higher foliage tolerance as well. In plants of chaparral vegetation, Valladares and Pearcy (1999) highlighted the influence of leaf orientation on the heterogeneity of the light environments; upper, south-facing leaves intercepted greater daily light than leaves of any other orientation. For many coniferous species (ponderosa pine, Douglas fir and western hemlock), the distribution and arrangement of foliage on shade shoots can greatly increase light interception, and therefore photosynthesis in the lower canopy (Bond et al. 1999). Needle clustering and penumbral effects of small size leaf also affect light penetration, interception, and photosynthesis (Stenberg et al. 1999).

Variation of light resources in the understory environment might also be observed in relation to the leaf phenology due to the seasonality that differs among species (Gendron et al. 1998, Hart and Chen 2006). Before leaf expansion, and following leaf senescence, deciduous canopies have much higher light transmission than all other stand types (Ross et al. 1986). Even for that reason deciduous forests are considered to have a marked seasonal light variability than evergreen forests (Gendron et al. 2001, Yirdaw and Luukkanen 2004).

Komiyama et al. (2001a) reported that differential overstory leaf flushing patterns contributed to the formation of a patchy understory. Also Kato and Komiyama (2002) found that the heterogeneity of light conditions that occurred in a deciduous broadleaved forest in late spring resulted from the different timing of leaf flushing by different tree species. In particular, heterogeneity is the main cause of the patchy distribution of understory plants. Effectively, direct spring sunlight penetrating should result in a positive correlation in terms of spatial distribution between late-flushing trees and understory plants (Komiyama et al. 2001a).

In general, we can sustain that species-specific attributes, such as crown structure, determine significant effect on the amount, quality and spatial variation of light transmittance (Yirdaw and Luukkanen 2004, Pretzsh et al. 2014) and consequently a simple but profound effect on forest succession (Canham et al. 1994, Canham et al. 1999). For example, crown depth (Canham et al. 1994, Beaudet et al. 2002, Beaudet et al. 2011, Ametzegui et al. 2012) and crown width (Canham et al. 1999), which were higher in shade tolerant species, influences the ratio of PAR to global radiation inside the canopy (Ross and Sulev 2000). Nevertheless, size and spacing of the crowns, or rather canopy openness, regardless of species, were of primary importance to the interspecific variation in openness of individual crowns, (Canham et al. 1999, Beaudet et al. 2002), revealing as a good predictor of the below-canopy transmitted diffuse and global solar radiation in old-growth and uneven-aged evergreen forest (Promis et al. 2009).

The crown structure of a tree is even more crucial in mixed stands where different species demonstrate their abilities to acclimate their structures in order to benefit of the resources more efficiently or obstruct the access of competitors to the same resources (Pretzsch 2009, Bayer and Pretzsch 2013). A morphological plasticity may results in crown and canopy structures in mixed stands which differ considerably from those observed in pure stands.

Effectively, in pure stands all individuals compete with similar behavior for the growing space and resources involving a homogenization of canopy structure with low canopy depth and size-asymmetric competition (Grams and Andersen 2007). Differently, in mixed stands the complementarity of species in terms of light ecology allow trees to have more canopy space to occupy without mechanical abrasion or penetration of neighboring crowns (Pretzsch 2014). However, the ability of trees to intercept light decreases with environmental stress (Waring and Schlesinger 1985). In general, light transmission is higher for species of Boreal forests other than for species in warmer and wetter temperate deciduous forests or conifer forests of the Northwestern America (Lieffers et al. 1999).

Mensurational attributes of stands and understory light

Understory light availability, frequently expressed as canopy openness (the proportion of the sky hemisphere not obscured by vegetation when viewed from a single point; Jenning et al. 1999), is a measure of great utility to foresters since it can be used to guide the level of canopy manipulation necessary for successful natural regeneration.

Understory light and its spatial distribution can be manipulated, at least in part, by designing and shaping harvesting according to the overstory structure of a forest stand (Battaglia et al. 2002, Beaudet et al. 2011). Therefore, knowing the interplay between stand structure and light is fundamental for managing forests. An accurate description of allometric functions and their relationships with radiance would provide foresters precious information for silvicultural decisions. Among stand structural attributes determined from readily available field data, those describing stand density, such as sum of DBH, basal area and number of trees, are usually the most considered in similar studies. For example. Comeau et al. (2001) observed that in white spruce-aspen dominated boreal mixed stands with high initial tree densities, the decline in understory light levels is likely to occur more rapidly, resulting in the potential for substantial reductions in growth and survival of understory spruce due to competition for light and physical damage to spruce as a consequence of aspen mortality by self-thinning. At another level, Drever and Letzerman (2003) found a significant correlation in a coastal Douglas fir forest in British Columbia between light transmittance and stem density, volume of retained trees, summed DBH and summed height. However, the predictive capacity of these variables was much better for high light levels (> 50 % of full sun) than for low levels of light (< 20 % of full sun).

Basal area is frequently used as independent variable to explain light transmittance through the canopy (Nilson et al. 1999), although the radiative transfer may differ between young and old stands and the possible difference of overstory structure and site conditions should be considered (Comeau et al. 2001). In mixed-species forests plot basal area should be not enough informative and separate coefficients should be developed for each species, at least the dominant species: this was the case of mixed aspen-conifer forests in British Columbia (Comeau et al. 2006) where basal area of deciduous species was significantly related to understory light, unlike conifer basal area. This contrasted with results from birch-conifer stands in the same areas, where the inclusion of conifer basal area improves the relationship with light. In another study, Sonohat et al. (2004) found a negative exponential relationship between light transmittance and stand basal area in even-aged stands of Douglas fir, Norway spruce, larch and Scots pine, which explained between 56% and 80% of transmittance variation according to the species, and 82% for all species pooled data.

Such relationship between basal area and canopy transmittance was often explored in relation to silvicultural practices. In the case of Sitka spruce thinned stands, studies have individuated a basal area < 30 m^2/ha to provide the minimum light requirements, i.e. 15% of incident light, for the growth of Sitka spruce seedlings (Hale 2001, Hale 2003, Page et al. 2001, Malcom et al. 2001). However, some authors (Beaudet et al. 2011, Battaglia et al. 2002, Sprugel et al., 2009), showed that harvesting in a stand does not necessarily increase light transmission proportionally to the reduction in basal area. In effect, the spatial arrangement of the residual trees (and hence the spatial pattern of harvest) also plays a very important role. Battaglia et al. (2002) demonstrated that increasing the aggregation of residual basal area, not only increases the mean stand level understory light availability but also increases the variation of light resulting in more heterogeneous understory light environments.

In old growth and second growth forests in lowland Costa Rica, Montgomery and Chadzon (2001) did not find strong relationships between measures of forest structure and light availability, although the strength of these relationships differed between forest types. In both the studied forests, understory light availability at 0.75 m decreased with increased sapling and shrub density, but was not significantly influenced by local tree density or basal area. Similar trends were found in an old-growth and uneven-aged forest of *Nothofagus betuloides* (Promis et al. 2009). However, by combining basal area, crown projection, crown volume, and stand volume, it was possible to explain a large amount of the variability of the below-canopy transmitted, diffuse and global radiation.

A study carried out by Valladares et al. (2006) in the holm oak (*Quercus ilex*) woodlands of the Western Mediterranean basin, characterized by low mean canopy height (2.4 m), high stem density (14,500 stems ha^{-1}) and intermediate basal area, showed that canopy height exhibited a more significant correlation with understory light (particularly with indirect light), than stem density and basal area although only in the tree-dominated zone of the plot. However, since the potential of canopy height as a predictor of understory light was low due to the large fraction of unexplained variance, the incorporation of other canopy features (e.g. leaf angle distribution, leaf and branch clustering) would likely increase significantly the accuracy of the estimation of understory light based on canopy structure.

Results from a study by Heithecker and Halpern (2007) suggested that levels of light at the forest floor within aggregate retained trees can be surprisingly similar to those inside the forest; the aggregates significantly reduced Photosynthetic Photon Flux Density PPFD) in the adjacent harvested area to distances of 10-30 m.

Therefore, it is evident that spatial aggregation or rather the spatial distribution of stem density for retained trees strongly regulates the abundance and spatial variation of light in the understory (Coates et al. 2003). Changes concern the quantity and quality of light, as well as its directionality, so that more of the forest floor receives direct solar radiation and sunflecks become longer and more intense (Lieffers et al. 1999, Gendron et al. 2001).

Conclusions

The many studies concerning the relationships between transmittance and structural attributes in forest stands carried out over the last two decades confirmed the great interest in predicting understory light conditions by using attributes readily available from field data. Different bioclimatic zones (boreal vs tropical), stands structure (plantation vs natural, even-aged vs uneven-aged, young vs old-growth), species composition (pure vs mixed), and silvicultural treatments (clearcutting vs partial cutting) were taken into account in these studies. However, most of the research was carried out in boreal forests, likely because light was considered one of the most critical factors for successional dynamics in this environment.

On the whole, the results of the examined studies highlighted that different traits of forest overstory affect light intensity in the understory, even more in heterogeneous stands with continuous canopy cover. Composition, density and structure of overstory are the characteristics mainly correlated to light transmittance (Fig. 1).

The weight of each of them seems to depend on the degree of complexity of the stand. In evenaged, unthinned and monospecific stands with homogeneous canopy covers and regular spatial distribution of trees, understory light conditions much depend on species specific traits such as shade-tolerance, which in turn is strictly linked with crown properties (depth, width, leaf angle distribution, etc.). In regular mixed forests, tree composition controls the amount of radiance under the canopy and the spatial and temporal distribution of light especially if evergreen and deciduous species or deciduous species with different phenology are a significant part of the mixture. In managed forests, canopy openness can be manipulated by silvicultural practices changing stand density attributes; basal area is amongst the most important in predicting light as long as understory radiation fall above 20% and especially

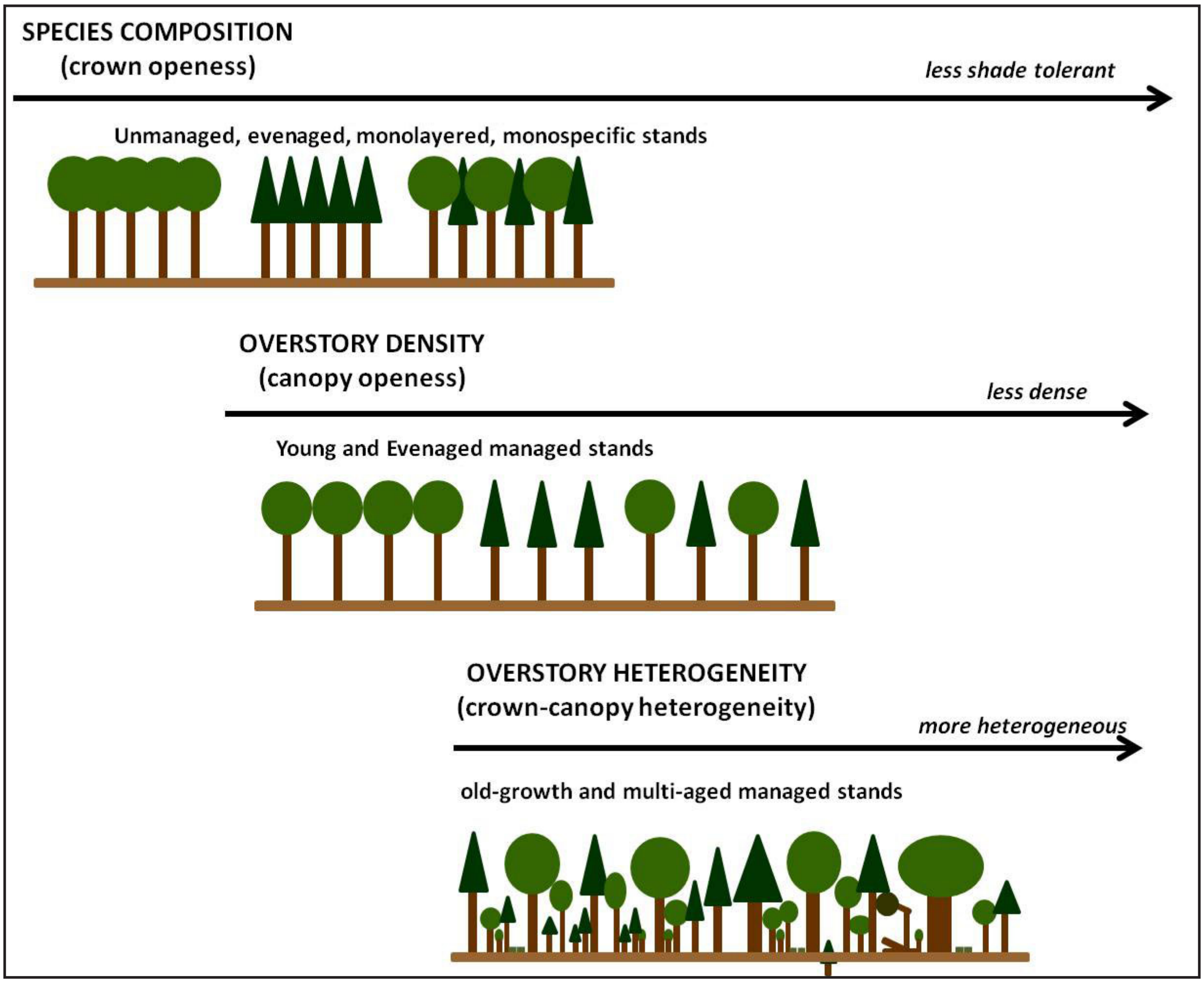

Figure 1: Diagram showing the three stand overstory characteristics affecting understory light.
When the stand profile is closed, simple, homogeneous the passage of light through the canopy depends on the characteristics of the crowns, then on tree composition. When silvicultural practices open the crown cover, composition being the same, stand density comes into play too. In forests with heterogeneous structure the light in the understorey is the result of the variability in the arrangement of stems in space and their size, which is added to the composition and density.
The weight of tree composition is higher in populations of tolerant species, that of density in the more open stands, that of structure in the very heterogeneous forest.
The three profiles are staggered to highlight that the three factors add up and interact with increasing diversification of the profile.

in young stands. Harvesting does not necessarily increase light transmission proportionally to the reduction in basal area and spatial arrangement of the residual trees plays a very important role (Beaudet et al. 2011, Battaglia et al. 2002, Sprugel et al. 2009).

For low average light levels typical of uneven-aged and old-growth forests, horizontal and vertical stand structure attributes need to be considered for increasing the accuracy of prediction. In such conditions, light transmission through canopy and the occurrence of patchy or homogeneous understory is controlled by the complex interplay of overstory composition, density and structure.

In conclusion, basal area can be viewed as the preferable light predictor for managing young stands with homogeneous structure. The experiences suggested considering additional parameters descriptive of tree size, such as DBH, height and volume, in order to increase the accuracy of light predictions in case of older stand or in presence of a layer of suppressed trees.

A different and more complex task is providing a significant estimate of radiation below canopy in stands characterized by heterogeneous vertical and horizontal structures. The few studies carried out until now didn't provide a clear overview of appropriate attributes for an accurate prediction of understory light in these types of forest structure. Therefore, considering the increasing importance of creating and maintaining stand structure heterogeneity through silvicultural treatments in order to enhance the resilience of forest ecosystems facing the global change, more research would be necessary to deepen this topic.

The continuous development of technologies is increasingly allowing their access to researchers and forest managers with relative low costs. The use of proximal and remote sensing technologies (Aschoff et al. 2004, Chianucci et al. 2014a, Danson et al. 2007, Maas et al. 2008) could represent in the future a valid solution for improving this type of studies and integrating field data with a more detailed information of canopy structure.

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